INHERITANCE IN CANARIES

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INHERITANCE IN CANARIES.

A. STATEMENT OF PROBLEM.

The objection has been raised that much of the material used in studies of heredity has been long under domestication, in consequence of which, first, extensive hybridization has occurred, and, secondly, characteristics of an "abnormal" sort have been preserved, and, as a result, conclusions drawn from such material can not properly be applied to feral species as they are evolving "in nature." It is extremely doubtful if this objection has any validity, as I have argued elsewhere (1906). Nevertheless it is well to study heredity widely and to include in the study some undomesticated and semi-domesticated species. On this account, four years ago I began the breeding of certain cage-birds and especially the canary bird (*Serinus canarius*).

The canary is, it is true, a semi-domesticated animal. I say semi-domesticated, for in domestication there are all degrees. The essence of domestication from the standpoint of heredity is long-continued control by man of mating. Many species of birds have been bred in zoological gardens, and various finches—linnets, siskins, goldfinches, bullfinches, etc.—are bred in confinement by fanciers and for commercial purposes. Likewise grouse and quail and numerous species of swimming birds have been kept captive through many generations, yet such acclimated animals are ordinarily not regarded as domesticated, because the breeding has not been long enough continued nor rigidly enough controlled to produce a number of varieties. Between such acclimated wild species and thoroughly domesticated species, such as poultry, dogs, sheep, and horses, which are hardly to be found in the wild state, the canary occupies an intermediate position.

The history of the canary in captivity is given as follows:* It occurs as a wild species in the Canary and the Madeira Islands. The wild species agrees in coloration so completely with the captive "green" canary with greenish-yellow breast and without white on remiges and rectrices that only a person with precise and thorough knowledge of both can find any certain distinguishing characteristic. After the Spaniards took possession of the Canary Islands in 1478 they brought many of the products of the islands home, and among others these remarkable songsters; but for a long time they were rare in Europe.

*The history has been written by Boile.

Konrad Gesner, who mentions the bird in his book "De Avium Natura," of which the first edition was published in 1555, had never seen it. According to Olina (1622) only males were, for many years, imported, but in the middle of the sixteenth century a Spanish ship, which presumably carried also some female canaries, was wrecked near the Isle of Elba, and the birds escaped, and populated it and created there a peculiar strain in that they were yellower beneath the chin than those brought directly from the Canary Islands. These birds of Elba were trapped by the Italians, bred in captivity, and sold in Italy, in the Tyrol, and in Germany, in which latter country they were already being bred in captivity in many places in the middle of the seventeenth century. Already at the beginning of that century Aldrovandi had been able to get the bird as a basis for a figure in his Ornithologiæ (1599–1603). From Germany the canaries were, in the middle of the seventeenth century, exported to England and other countries and were already regarded as improved over the wild species,* but their color was still green.†

The spread of canary culture was aided by the fact that they became a society fad. Owing to their high price, they were attainable only by the wealthy and so became a mark of that class. Ladies received visitors with a canary perched on the index finger and were painted in that attitude.‡

From the beginning of the eighteenth century there is a constantly increasing output of books devoted to cage-birds in general and canary birds in particular,§ so that it is possible to reconstruct their history.

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*In Willoughby's Ornithology (Ray, 1678), quoting an earlier English author, it is stated: "Canary birds of late years have been brought abundantly out of *Germany* and are therefore now called *German* birds; and these *German* birds in handsomeness and song excel those brought out of the Canaries.

†In "The Gentleman's Recreation," published in 1677, we find that at that date canaries in England were of a green color. (See Blakston, Swaysland & Wiener, 1880, 5.)

‡In the New York Public Library is a little sociological tract entitled, "Canary Birds Naturalized in Utopia: A Canto." London, *ca.* 1708. The canto begins:

> In our unhappy days of *Yore*,
> When foreign *Birds*, from *German* Shore,
> Came flocking to Utopia's Coast,
> And o'er the Country rul'd the Roast:—
> Of our good People did two-thirds
> So much admire Canary Birds
> For outward Show, or finer Feathers
> Far more regarded than all others.
> We bought 'em dear and fed 'em well,
> Till they began for to rebel.

§The most famous of early works is that of J. C. Hervieux: "Nouveau traité des Serins de Canarie, contenant la manière de les & élever les appareiller pour en avoir de belles races; avec des remarques aussi curieuses que nécessaires sur les signes et causes de leur maladies et les secrets pour les guérir." 12 mo., Paris, 1st edition, 1705 [5 editions to 1785]. This work was translated into English, German, and Italian.

First it appears that although in 1677 only green canaries were known, as early as 1713 three main color varieties had become established, in which various subvarieties are recognized. The whole series as given by Hervieux is as follows:

Serin gris	Serin blond doré
Serin gris aux pattes blanches	Serin blond aux duvets
Serin gris à queue blanche	Serin jaune commun
Serin blond commun	Serin jaune aux duvets (race de Panachés)
Serin aux yeux rouges	Serin jaune a queue blanche (idem)

Hervieux's "Serin gris" is doubtless of the wild type of coloration; our "green." The "jaune" is doubtless the modern clear or yellow type. Hervieux states that it is (in 1713) among the rare varieties. What the "blond" type is can only be conjectured, but it is probably our mealy, or light, yellow. If this inference is correct three of the modern colors of canaries—green, jonque yellow, and mealy yellow—made their appearance at about the end of the seventeenth century. Their appearance would seem to have been quite sudden—a result indicating their origin by mutation rather than by slow increments in the desired direction.*

It appears also that mottled or variegated birds (race de Panachés) were known, and as we shall see later they are probably the result of the crossing of a green bird and a yellow one. Such variegated birds were much esteemed in the early part of the eighteenth century. During the first half of that century the number of color varieties was greatly increased, since Hervieux, in his edition of 1766, recorded 29 color varieties including gris (green), blond (mealy yellow), jaune (jonque yellow), agate, isabella (buff or cinnamon), blanc (white), panaché (mottled), and plein—"qui est à present le plus rare."

The histories do not state when the crested form first appeared. Crested birds, like yellow ones, are now bred in captivity in their native islands. The frizzled characteristic found in the Parisian Trumpeter or Serin frisé or Dutch frizzle is probably relatively recent, as it is relatively uncommon. Likewise of the other varieties (lizards, albinos, etc.), the origin is quite obscure. The introducer of a new variety usually conceals its origin; indeed, he has little to say, as he does not produce or induce the new characteristic, but merely preserves that with which fortune has favored him.

The history of acclimated canary birds thus reveals their comparatively recent domestication and justifies the contention that their characteristics may well be expected to be inherited much as they would be if found in wild birds.

The specific characteristics upon which I propose to report in the present paper are two; viz., plumage-color and crest. The matters of

*Russ (1906, 6) concludes that the change from green to yellow certainly occurred quickly.

form and position, of frizzling, and certain others are not yet ready for a report. The types of color that I have studied most thoroughly are the original green and the yellow. These have been bred pure *inter se*, and with other species. The cinnamon and lizard-color types have been merely touched. As for the crest, this consists of a group of feathers on top of the head arranged so as to radiate from a center between the eyes and forming a small cap covering over the eyes and beak. The questions are: How is the crest inherited, and how is the plumage-color inherited?

B. MATERIAL AND METHODS.

My original stock (1904) consisted of 4 yellow hen canaries (one crested) of the short or German (Harz Mountain) type and 2 green birds of the same type. Also 3 yellow cocks (one crested) and 2 greens (one crested). To these each year sundry other canaries were added. These were purchased from a dealer in New York and had been imported from Germany or England.

The canaries were bred in a room at the Station for Experimental Evolution, each pair being kept in a separate cage. The usual methods of feeding were adopted. All birds bear numbered leg-bands by which their identity is established.

C. RESULTS.

Series I.—THE INHERITANCE OF CREST.

STATEMENT OF PROBLEM.

It is my experience with poultry (1906, 69) and pigeons that *crest* is alternative in heredity and dominates *absence of crest.* I wished to test heredity of crest in canaries also to see whether the conclusion that I have elsewhere (1906, 87) reached holds, viz., "dominance and recessiveness depend upon a relation of the characteristics *per se* and not upon any relation of the races into which they have been introduced."

MATERIAL.

Crested and plain Harz canaries were chiefly used, but also a few of the "Norwich" type, which had a flatter and darker crest (plate 1, fig. 2).

RESULTS.

It quickly appeared that crest is alternative in inheritance, for when crested and non-crested birds were paired, the offspring were either well crested or plain-headed and there were no intergrades. This leads to the hypothesis that crest is dominant as in poultry and pigeons. To test this hypothesis I made a number of matings, of which the detail is given in Section E.

1. Recessiveness of Plain Head.

The following table contains, extracted from the general table, those experiments that give an answer to the question whether non-crested heads are recessive to plain heads. All parents are non-crested.

Table 1.—*Progeny of Non-Crested Parents.*

[The superior and inferior letters C (crested) and c (non-crested) indicate the condition of the grandparents. o signifies original stock, of whose ancestry, consequently, nothing is known directly. The numbers in columns "Father" and "Mother" are those of the leg-bands.]

Experiment No.	Mother.	Father.	Crest.		Experiment No.	Mother.	Father.	Crest.	
			Absent.	Present.				Absent.	Present.
401	7o	8o	1	0	618	52^{c}_{c}	75^{c}_{c}	8	0
404	17o	16o	2	0	619	64^{C}_{C}	85^{C}_{c}	11	0
405	19o	20o	2	0	623	74^{C}_{C}	77^{c}_{c}	8	0
501 } 514 }	4o	37^{c}_{c}	11	0	624	78^{c}_{c}	37^{c}_{c}	3	0
507	18o	46o	1	0	711	152^{c}_{c}	215^{c}_{c}	2	0
512	101o	8o	3	0	716	210^{c}_{c}	185^{c}_{c}	3	0
605	89^{c}_{C}	8o	9	0	718	132^{c}_{c}	201^{c}_{c}	2	0
609	84^{C}_{c}	65^{c}_{C}	8	0	719	100^{c}_{c}	135^{c}_{c}	2	0
612	76^{c}_{c}	51^{c}_{c}	1	0	721	339o	209^{c}_{c}	8	0
613	7o	39^{c}_{c}	1	0	723	200^{c}_{c}	142^{c}_{c}	5	0
614	53^{c}_{c}	28o	8	0	725	112^{c}_{C}	105^{c}_{c}	1	0
615	100^{c}_{c}	37^{c}_{c}	2	0					
						Total		102	0

Thus of 102 offspring of two non-crested parents all were non-crested. In table 1 are included several cases—Experiments 605, 609, 619, 623, and 725—where from one-fourth to three-fourths of the grandparentage is crested. In these experiments Galton's law calls for an average of *at least* 22.5 per cent (and at most 45 per cent) crested offspring. The 37 offspring *are all non-crested.* Galton's law simply does not apply to cases of alternative inheritance.

2. The Detection of Homozygous Crests and the Gametic Composition of Heterozygotes.

If crest is an alternative characteristic we should expect to find some (one in three) homozygous dominants which always throw only crested birds, whether mated with a crested or a non-crested bird. The following experiments were arranged to test the purity of crested birds.

TABLE 2.—*To Test the Purity of Crested Parents.*

[Leg-band numbers in italics indicate non-crested birds. Arbitrary signs employed in this table have the same meaning as in table 1.]

I. BOTH PARENTS CRESTED.					II. ONLY ONE PARENT CRESTED.				
Experiment No.	PARENTAGE.		CREST.		Experiment No.	PARENTAGE.		CREST.	
	Mother.	Father.	Absent.	Present.		Mother.	Father.	Absent.	Present.
403	21o	13o	1	1	402	*10*o	9o	0	1
504, 510	6o	9o	1	10	502	44^{c}_{C}	*16*o	2	5
506	12o	13o	0	2	503, 511	3^{C}_{c}	*4*$^{c}_{c}$	4	5
508, 515	11o	13o	1	3	505, 515	7o	34^{C}_{C}	3	5
601	12o	73^{C}_{C}	0	7	514	*31*$^{c}_{c}$	50o	2	2
608	67^{c}_{C}	9o	0	5	604	*19*o	62^{C}_{C}	7	1
610	54^{C}_{c}	61^{C}_{C}	0	2	606	*39*$^{c}_{c}$	68^{c}_{C}	9	1
611	97^{C}_{c}	34^{C}_{C}	3	0	613	*55*$^{C}_{c}$	50o	7	1
617	82^{C}_{C}	79^{C}_{C}	0	4	625	*33*o	87^{C}_{c}	3	1
620	69^{C}_{C}	83^{C}_{c}	3	2	704	*19*o	79^{C}_{C}	0	7
621	81^{C}_{C}	58^{C}_{c}	1	5	705	127^{C}_{C}	*125*$^{C}_{C}$	3	5
701	207^{C}_{C}	61^{C}_{C}	3	1	706	126^{C}_{C}	*214*$^{C}_{C}$	0	4
702	—o	269o	1	1	707	*71*$^{C}_{C}$	206^{C}_{C}	1	1
703	67^{c}_{C}	166^{C}_{C}	3	7	708	*138*$^{C}_{C}$	73^{C}_{C}	2	4
710	97^{C}_{c}	34^{C}_{C}	0	3	709	111^{c}_{C}	*145*$^{c}_{c}$	4	0
710a	164^{C}_{C}	118^{c}_{C}	0	2	712	178^{C}_{C}	*107*$^{c}_{C}$	4	4
713	157^{c}_{C}	240^{C}_{C}	1	6	717	—o	—o	1	1
			18	61	720	193^{c}_{C}	*169*$^{c}_{c}$	0	1
								52	4_9

Inspection of table 2 shows that at least 2 birds are homozygous in crest, viz., No 12 (female), which has produced 9 young, all crested, and No. 79 (male), which has produced 11 young, all crested. Also No. 126 (female) (Experiment 706) is possibly homozygous. No. 9 (male) has produced an unexpectedly large proportion of crested, viz., 16 : 1, where 12.75 : 4.25 was to be expected; mated with No. 6 (female), No. 79 (male) was produced which is, as just stated, homozygous.

When two heterozygous crested (DR) parents are mated 25 per cent of the offspring should be non-crested. Eliminating the offspring

of Experiments 506, 601, and 617 (with one parent homozygous) we have totals of 18 non-crested to 48 crested offspring, while theory calls in this case for 16.50 and 49.50 respectively. The actual result accords closely with expectation.

When a heterozygous crested (DR) parent is mated with a non-crested (R) one, 50 per cent of the offspring should be non-crested. Subtracting from the totals of the right half of table 2 the offspring of homozygous 79 (male, Experiment 704), we get 52 non-crested to 42 crested, instead of the expected 47 and 47. The considerable deviation from expectation is doubtless due to insufficient numbers and the extraordinary run of excess of non-crested offspring obtained in Experiments 604, 606, and 613.

3. Baldness.

It is frequently stated (Kidd, teste Darwin, 1876, chap. VIII; Russ, 1906, 127–128) that two crested birds should not be mated together because they rarely produce fine crests, but, on the contrary, bald heads. One is advised to mate the crested bird with a non-crested one whose parents were crested. Blakston (1880, 129), while approving this rule of breeding, scouts the idea that the produce of two crests tend to be bald. Such produce tend merely to have high tufts instead of the desired *flat* crests. The experiments listed in table 2 are of a sort to throw light on this question. Are the 61 crests derived from the experiments recorded on the left hand of the table different from those derived from Experiments Nos. 505, 515, 604, 704 to 708, and 712, recorded on the right hand of the table? An examination of the distribution of bald offspring does not show that they are confined to or exceptionally prevalent in the cases of matings of two crested individuals. It is necessary to seek another cause for baldness.

An inspection of the records shows: first, that of my original crested birds some had a perfect (or fully feathered) crest and in others the crest was imperfect (*i. e.*, more or less bald on the occiput). Birds with perfect crest were Nos. 9 (male), 11 (female), and 34 (male), while birds with imperfect crest were Nos. 3 (female), 6 (female), 12 (female), 13 (male), and 21 (female). Now, with one exception (see Experiment 714), all of the bald offspring obtained in these experiments had one of the imperfectly crested birds in its ancestry. This fact suggests the hypothesis that imperfect crest is a unit-character in heredity. To test this hypothesis I have made various matings between individuals with and those without an imperfect crest. The results of such matings are given in table 3.

TABLE 3.—*Matings to Test Inheritance of Imperfect Crest.*

Experiment No.	Mother. No.	Mother. Perfect (P) or Imperfect (I) Crest.	Father. No.	Father. Perfect (P) or Imperfect (I) Crest.	Offspring's Crest. Perfect.	Offspring's Crest. Imperfect.	Non-Crested.
A. BOTH PARENTS HAVE IMPERFECT CREST. (RR × RR).							
506	12	I	13	I	0	2	. . . . .
617	84	I	79	I	0	1	. . . . .
620	69	I	83	I	0	1	3
Total . .	. . . . .	. . . . .	. . . . .	. . . . .	0	4	3
B. NEITHER PARENT HAS IMPERFECT CREST. (α) DD × DD or DD × DR.							
505	7	. . . . .	34	P	4	0	4
610	54	P	61	P	2	0	. . . .
613	*55*	. . . . .	50	P	1	0	7
625	*33*	. . . . .	87	P	1	0	3
713	178	P	*107*	. . . . .	4	0	4
Total . .	. . . . .	. . . . .	. . . . .	. . . . .	12	0	18
(β) DR × DR.							
705	* 127	P	* *125*	. . . . .	5	2	3
707	* *74*	. . . . .	* 206	P	1	0	1
708	*138*	. . . . .	* 73	P	1	1	2
714	157	P	240	P	4	1	1
Total . .	. . . . .	. . . . .	. . . . .	. . . . .	11	4	7
C. ONE PARENT HAS IMPERFECT CREST. (α) DR × RR.							
508	11	P	13	I	1	1	. . . . .
510	6	I	9	P	0	4	. . . . .
515	11	P	13	I	0	1	. . . . .
603	11	P	80	I	2	1	. . . . .
604	*19*	. . . . .	62	I	1	1	7
608	67	I	9	P	2	2	. . . . .
703	67	I	166	P	3	1	3
704	*19*	. . . . .	79	I	5	2	. . . .
706	126	I	*214*	. . . . .	1	3	. . . . .
711	164	I	118	P	1	1	. . . . .
Total . .	. . . . .	. . . . .	. . . . .	. . . . .	16	17	10
(β) DD × RR.							
504	6	P	9	I	2	0	1
513	7	P	34	I	1	0	. . . . .
622	81	I	58	P	4	0	. . . . .
720	193	I	*169*	. . . . .	2	0	. . . . .
Total . .	. . . . .	. . . . .	. . . . .	. . . . .	9	0	1

* These birds are known to have imperfect-crested ancestors; the others probably have.
Italic numbers are those of non-crested birds.

Table 3 shows that when two imperfect crests are mated the offspring have imperfect crests (table 3, A). This indicates that absence of occipital feathering is recessive (R) to its presence. When perfectly feathered individuals that are probably hybrids between dominants (D) and recessives (R), *i. e.* DR's, are mated with imperfectly feathered consorts (RR) an equal number (16 : 17) of perfectly crested and imperfectly crested are thrown (table 3, C, α). When two heterozygous individuals are mated there result about 75 per cent perfectly crested offspring to 25 per cent imperfectly crested—actually 11 : 4 (table 3, B, β). When a pure dominant is mated to a pure recessive all offspring are perfectly crested (table 3, C, β). When both parents have a perfect crest (being, therefore, DD or DR) all offspring have the perfect crest (table 3, B, α). Altogether it appears that, *in crested birds*, absence of feathers on the occiput is recessive to their presence. Consequently we have in the crest two pairs of allelomorphs: crest *C* and absence of crest *c*: occipital feathering *O* and absence of occipital feathering (baldness) *o*. Then *CO* is the zygotic formula for perfectly crested, *Co* for imperfectly crested, *cO* for the ordinary plain-head, while a fourth possible combination, *co*, should occur in one-sixteenth of the offspring in F_2 and should be partly bald plain-heads. This combination I seem not yet to have acquired nor have I seen it mentioned; yet it is to be expected. Nevertheless it is possible that baldness is coupled with crest.

The Mendelian nature of the inheritance of baldness sufficiently explains the view of some canary breeders—cited at the beginning of this section. For two crested parents may throw from 100 per cent to 25 per cent bald offspring according as they are RR or DR in respect to baldness. But, since all crestless parents are DD or DR in respect to baldness, a crested bird mated with a crestless can give at most only 50 per cent bald-headed and may give none at all.

Series II.—THE INHERITANCE OF PLUMAGE-COLOR.

STATEMENT OF PROBLEM.

We have seen that the original canary was "green" and that out of such a pigmented canary there was evolved, over two centuries ago, a yellow race. Although the historical evidence is incomplete it favors the view that the yellow form arose suddenly, as a sport. Similarly, within recent years, in the Australian grass parakeet, or budgerigar, a yellow variety has arisen under domestication. The interpretation of these color changes must rest on the facts of chemical physiology. According to Krukenberg (1882, 21) there is no green pigment in the wild canary, but the green is due to a yellow and a dark pigment. The yellow pigment is of a fatty nature, is easily extracted by boiling

alcohol or ether, and is classified as a lipochrome (zoofulvin). The "green" barbs from which the lipochrome has been extracted are dark-brown or black. This dark pigment is much more resistant to reagents and is a melanin having its locus in minute granules. It was the purpose of the hybridization experiments to learn how these two kinds of pigments are inherited.

In addition to green and yellow canaries there is a color variety known as "cinnamon." A microscopic examination of the barb shows that the quantity of pigment in the quill feathers of the cinnamon is much less than in the "green"—and is probably of a different quality, being allied to the buff of pigeons and poultry. A fourth color type is the "lizard." This is a special pattern rather than color, to which further reference is made below.

A word about nomenclature is necessary, and in this I follow mainly Blakston. There are two grades of concentration of all colors—the dense, bright shade or "jonque" color, and the dilute, dull tint or "mealy" color. A "self" yellow, green, or cinnamon is of approximately one color all over—though with varying shades and tints. A yellow mixed with black over a varying extent of the body is called mottled or pied. "Heavily variegated" birds have breast, back, wings, and tail dark; "lightly variegated" birds have only back, wings, and tail dark; "marked" birds have wings and tail dark and no melanic pigment on the body excepting eye-stripes; "ticked" birds are all yellow, except for small patches of dark color.

RESULTS.

1. On Inheritance of Green and Yellow Plumage-Color.

Breeders of canaries for color have formulated certain directions to be followed in the work. Those of Russ (1906, 125–127), one of the best-known authors on cage-birds, are, on account of their definiteness, worthy of translation here.

> Experienced breeders have demonstrated that in color-breeding the choice of the male is determinative, while the female must be self-colored. Thus, *e.g.*, to produce crested offspring with a high yellow color one selects a male of this color, but a green, non-crested female. The more purely thoroughbred the birds are, *i. e.*, the greater the number of generations they have been held pure, the purer their progeny. Let a yellow pair, no matter of what origin, from green or gray, produce young among which is a yellow male; let this breed next year, in a separate cage, with a yellow female; young are produced among which is a yellow male. If such a male be mated with a female likewise bred true for two generations, their progeny will never produce anything but yellow offspring. If one collects three or four pairs of this sort and lets them fly free in the room there need be no fear that any discolored birds will be produced. . . . The same holds true for all self-colored varieties; for the bright-yellows, straw-yellows, whites, greens, grays, and isabella-colored, but not for mottled birds. The latter are far more subject to accidental variation, and one may be happy

to obtain from four or five broods one "Ausstich," *i. e.*, a beautifully "*marked*" bird. Here also is it very important that two pure-bred birds be mated, *e. g.*, a beautiful crested green cock with a straw-yellow female; most of the progeny will then resemble the parents, and be likewise uniformly green or yellow: but if a mixture of color does occur it will usually be an "Ausstich." Such "Ausstichvögel" are used . . . . for the production of rare markings. Green and isabella colors do not mix, *i. e.*, these two colors do not occur in the same bird; paired they produce only young which show each color alone. Finally, the following results of crossing seem to have been demonstrated. Black and green capped birds are bred from a male of this sort mated with a pure yellow female; green or black "swallows" from a gray or blackish-green crested male with a non-crested bright-yellow female; isabella "swallows" from a crested isabella male with a golden yellow non-crested female, and gray-, green-, and black-crested from a male of the required sort with a bright or a straw-yellow female.

My own experiments in part confirm these statements, in part disagree with them. These results are as follows:

a. Green × *Green.*—When self-greens are mated together all of the offspring are green. I made five matings of this sort (Nos. 402, 404, 502, 613, and 624) and obtained 21 green offspring and no other color.

b. Yellow × *Yellow.*—When self-yellows are mated together all of the offspring are yellow. I made 11 matings of this sort and obtained 34 offspring; all were pure yellow except in 6 cases, where there were tickings of a darker color. These were obtained in Experiments Nos. 503 (2), 513 (1), and 606 (3). As to Experiment 606 it should be said that No. 68 (male) used in it, though yellow, had a green crest and a green patch lying off of the crest on the nape of the neck.

c. Yellow × *Green.*—This cross,* no matter what the ancestry of the colors, invariably gave mottled birds with varying proportions of dark pigment on the yellow background. At one extreme are the "heavily variegated" birds; at the other extreme is only a "ticking." The usual result is a "lightly variegated" or unsymmetrically "marked" bird. The distribution of the dark pigment is not wholly at haphazard. Green is usually found in the lateral tail feathers, on the secondaries and wing-coverts of one or both wings. In addition to these areas patches are found on the head, nape, breast, at the base of the circumanal feathers, between the shoulders, and on the rump. The crossing of yellow and green thus gave me, in disaccord with the statement of Russ above, *always* the mottled condition (plate 3, fig. 5).

It now remained to determine the nature of the mottled condition—whether a fixed mosaic or, like the blue color of Andalusian fowls, a heterozygous form or, like mottling in mice, due to a mottling factor. Consequently, I mated the mottled birds of F_1 with each other, with greens, and with yellows. The results of such matings are given in tables 4 and 5.

* Experiments 501, 504, 506, 508, 509, 510, 512, 514, 515, 608, 611, 710.

TABLE 4.—*Mottled* X *Mottled.*

[G, green; Y, yellow; M, mottled.]

Experiment No.	MOTHER.		FATHER.		OFFSPRING.		
	No.	Prevailing Color.	No.	Prevailing Color.	Yellow.	Green.	Mottled.
610	54	G	61	G wings	0	1	1
617	82	Y	79	G	0	1	0
618	52	Y	75	Y	3	0	5
621	81	Y	*58	Y	1	0	4
623	74	G	77	Y	0	0	8
705	127	Y	125	G	5	1	2
706	126	Y	214	Y	1	0	3
708	138	G	73	Y	0	2	2
715	184	G	103	Y	0	0	1
716	210	Y	186	Y	0	0	3
718	132	Y	201	G	0	0	2
719	100	Y	135	Y	0	0	2
723	200	G	142	Y	3	1	1
					13	6	34

* No. 58♂ is of Y X Y origin, but has a green nape, perhaps derived from the green crest of its mother.

Table 4 shows that mottled coloration yields, upon inbreeding, the pure forms, yellow and green.

TABLE 5.—*Mottled* X *Self.*

[♂, male; ♀, female.]

MOTTLED X GREEN.						MOTTLED X YELLOW.					
Experiment No.	Mottled Parent.		Green No.	OFFSPRING.		Experiment No.	Mottled Parent.		Yellow No.	OFFSPRING.	
	No.	Prevailing Color.		Mottled.	Green.		No.	Prevailing Color.		Mottled.	Yellow.
601	73♂	Y	12♀	3	4	604	62♂	Y	19♀	6	4
603	80♂	G	11♀	1	2	605	89♀	Y	8♂	2	7
610	61♂	Y = G	54♀	1	1	612	76♀	G	51♂	1	0
615	53♀	G	28♂	5	3	619	64♀	Y	85♂	8	3
616	100♀	G	37♂	2	0	620	69♀	Y = G	83♂	3	1
624	78♀	Y	37♂	1	2	702	269♂	Y	Bel. ♀	0	5
701	61♂	G	207♀	3	1	703	28♂	Y	67♀	4	6
707	74♀	G	206♂	1	1	704	79♂	Y	19♀	4	1
711	164♀	G	118♂	*1	0	709	111♀	Y = G	143♂	4	0
714	240♂	Y	157♀	†4	2	720	193♀	Y	169♂	0	2
						725	112♀	Y	105♂	0	1
				22	16					32	30

*Also one yellow. †Also one yellow (?) died very young.

The experiments recorded in table 5 show that when the mottled form is mated with a pure yellow or a pure green the offspring are nearly equally of the two parental colors and none other.* Moreover, the extracted yellows are "pure," since when bred *inter se* they produce only yellows.

The interpretation of the results of breeding plumage-color is not difficult and may easily be brought to accord with Mendel's law. As already stated, yellow is "green" which has lost its melanic pigment. The mottled canary further differs from the green or the yellow in a spottedness like that of the spotted mouse; and as Cuénot (1903) has shown the latter to be due to a particular factor we may expect the same to be true for the canary. Calling the black factor *N* (nigrum) and the mottling factor *M*, we may assign to the green parent the gametic formula *Nm* and to the yellow parent the formula *nM*, *i. e.*, it contains the mottling factor, but lacks the melanin necessary to make it show. The gametic composition of F_1 is thus *NM nm* and the soma shows black in spots as a green on a background of yellow. On this assumption of two pairs of allelomorphs, we expect in every 16 birds of F_2: 9 mottled, 3 green, and 4 yellow, of which last class 3 are *nM* and 1 *nm*, without trace of the mottling factor. The observed result in F_2 agrees fairly well with this hypothesis. When mottled is mated with mottled we get, as table 4 shows, a total of 34 mottled, 6 green, and 13 yellow, expectation being 30, 10, and 13 respectively. The result departs from expectation in so far as there is a deficiency of greens, but a change of 4 individuals from mottled to green would establish complete accord with theory.

When a mottled bird is mated with yellow or with green expectation is an equal number of mottled and self-colored offspring. The number of offspring of each class derived from the mottled × yellow cross accords with expectation. Of 62, 32 are mottled and 30 yellow. Of 38 offspring of a mottled × green cross 22, or 58 per cent, were mottled and 16 green. Here, again, is a deficiency of greens, but not a very improbable one. Altogether, the results favor the hypothesis that there are in canary plumage two distinct and distinguishing factors—a black factor and a mottling factor.

2. Inheritance of Ticking.

It has been stated above that in mating yellow birds yellow offspring ticked with black were occasionally obtained. Similarly marked birds were obtained at other times. It seemed desirable to ascertain

* One clear exception and one doubtful one are found in the green × mottled matings of Experiments 711 and 714 where a yellow appeared among the offspring.

whether this ticking is an accident that may be eliminated by further dilution with yellow blood or darkening with "green" blood or whether it is a unit-character like mottling which persists, defying all attempts at dilution. The history of some matings to test this point is given in table 6, in detail.

TABLE 6.

Exp. No.	Mother.			Father.			Offspring.
	No.	From Exp. No.	Description.	No.	From Exp. No.	Description.	Nos. and Description.
621	81	510	Mottled	58	503	Y + N on nape	127, 129, 189, mottled. 188, Y + N patch at base of beak. 190, Y + N spots on head and nape.
605	89	513	Y + N patch on L nape	8	o	Y	168, 169, 170, 171, all Y. 135, Y + N spot on R nape and between shoulders. 136, Y + N spot on L wing.
721	339	o	Y	209	618	Y + N spot on R nape	271, 273, 317, all Y. 270, Y + spot under L eye. 272, Y + neck stripe, L side. 314, Y + spot at L ear. 315, Y + spot over each eye, on R nape and R secondaries. 316, Y + spot at L eye and on L wing.

Table 6 may be summed up in the statement that ticked yellow behaves like variegation; for ticked yellow × clear yellow gives 50 per cent ticked and 50 per cent pure yellow. Ticking differs from variegation only in the amount of dark pigments involved. We have already seen that there is probably a determiner for mottling. We now see that the mottling determiner occurs in various degrees which may be designated M′, M″, etc.

The question arises what determines the degree of mottling in any case? If all mottling results from a cross of yellow and green why are the proportions of yellow and green so diverse? Of the fact of this diversity there is no doubt. For example, in Experiment 501 a pure yellow (No. 4 female) was crossed with a pure green (No. 37 male), and of two offspring one was *green*, except for yellow bands across the back and a yellow belly and breast. The other was all *yellow* except for dark eye-spots, side of breast, and base of perianal fluff. Consequently one may speak of the mottling factor as wide in one case and restricted in the other. Individual germ cells vary in the extent of the spots they determine.

3. Inheritance of Yellow × Lizard Coloration.

The "Lizard" canary is closely related to the "Green;" it differs in that the margin of each of the dorsal body feathers is much lighter than the rest of the web—the feathers are "laced." This condition is dimly seen in the green canary, but is much exaggerated in the "Lizard." The light tip may be either yellow (jonque) as in the "Gold Lizard" or white (mealy) as in the "Silver Lizard." A second characteristic of the Lizard is a light area or "cap" on top of the head over the eyes, which, similarly, is either reddish or white. The characters of the Gold and of the Silver Lizard are said to be quite stable in straight breeding.

In my experiments (Nos. 507 and 512) I crossed a Gold Lizard (male) with a crestless yellow Norwich canary. One young was obtained. This had the yellow cap of the Lizard parent. The bird was mottled, but the dark feathers were laced (like those of the Gold Lizard) with yellow. When a Silver Lizard (female) was mated with a yellow Harz I got three young, closely alike. All had a cap, but this was yellow instead of silver. All were mottled and the dark body feathers were generally laced. It appears, therefore, from these few experiments, that cap and lacing are dominant over their absence and "gold" is dominant over silver, *i. e.*, jonque over mealy.

4. Inheritance of Cinnamon (Female) × Green (Male).

In canary hybridization cinnamon has long been known to behave in a peculiar way. A cinnamon male mated with a female of another race may produce some cinnamon offspring; but a pure non-cinnamon male mated to a cinnamon female produces no cinnamons. Also, the offspring of cinnamons bred to greens are often of a better cinnamon color than their parents. My own experience consists of two progeny of a cinnamon Belgium female × green Belgian male. Both are of a beautiful green color and show no trace of the cinnamon color. The female cinnamon seems to be fully recessive to green.

Series III.—INHERITANCE OF CHARACTERISTICS IN HYBRIDS BETWEEN THE EUROPEAN GOLDFINCH AND THE YELLOW CANARY.

The statement is frequently seen that it makes a great difference in heredity whether the individuals crossed belong to allied races or to distinct species. Focke (1881, 473) states that in race-hybrids characters of the parents do not blend as they do in species-hybrids. It is important to know if this law holds universally, and the finches offer a good opportunity to test it. They are easily hybridized and the results of such experiments have often been recorded by writers on cage-birds (*cf.* Blakston). The commonest of these hybrids is that

between the male goldfinch and female canary. These hybrids have been often described and they have been carefully analyzed by Klatt (1901), who used, however, only museum material or descriptions and knew little about the parents of the individual birds examined. Like all other writers on the subject, Klatt lays emphasis on the great variability of the first generation of hybrids—a variability which is in striking contrast to the uniformity exhibited by most first hybrids between domesticated races. The hybrids between the goldfinch and the canary are usually very dark—brown, black, and "green" predominating—but they usually show various yellow and white patches which may be very extensive and, in extreme cases, result in almost entire albinos. This variability demands an explanation.

The goldfinch (*Fringilla carduelis* Linnæus), as shown in plate 2, fig. 4, is marked on the head by a red patch on forehead and chin, a black eye-stripe and a black cap extending back on to the nape, where it is sharply cut off by a transverse white band. A pair of white areas run up from the throat on the sides of the head to the black cap. On the body, the back and sides are brown, this color extending also all over the breast and upper wing coverts. The rest of the ventral body is white. Yellow areas on the middle of the exposed portion of all quill feathers form in the folded wing a yellow wing band, and the quill feathers are tipped with white.

When such a goldfinch was crossed with a crested yellow Harz (plate 1, fig. 2) one of the hybrids was like plate 2, fig. 3. One can see at a glance that the hybrid is not a mere combination of the characters of the two parental forms, but is more like a *green* canary combined with the goldfinch. First, a rudimentary crest is present. The red of the face has become of a copper color (red + yellow) and the cap is dark greenish (black + yellow). The breast and belly are yellowish as in the "green" canary. The remiges are black with lighter tips—a modified goldfinch character. The yellow wing-bar is present, but reduced, combining the character of the goldfinch with that of the green canary. The sides of breast and wing-coverts are striped, due to a central blackening of the feathers—a character of the green canary. It thus appears that characters of the green canary predominate, but do not replace the more striking characters of the goldfinch.

The fact that the hybrids between the goldfinch and yellow canary have many of the distinctive features of the "green" canary has been frequently observed. Darwin, having heard of the streaked feathers of the hybrid, concluded that "this streaking must have been derived from the original wild canary;" and this case seemed to favor his theory of reversion. Klatt (1901, 508) goes further and concludes

that there is a reversion in some characters to the serin or Girlitz (*Serinus hortulanus* Koch), probably close to the ancestor of the wild canary. These characters are four: "in der breiten Binde der Spitzen der Armschwingen, den Flügelbinden der Deckfedern, den Farbung der Schultern, den Saumen der Steuerfedern." But in respect to the first and last of these characters I find in my birds no important difference from the green canary, except a slight yellowing of the lighter areas. The color of the shoulders of the hybrid is, as it were, the sum of the colors of the goldfinch and the canary. As to the second of the differential characters—the yellow wing-bow—this is highly variable in my hybrids and in mottled canaries. We have no reason to conclude that there is reversion to the serin, and it is undesirable to rest with so vague a term as reversion as an "explanation" of the resemblance of the hybrid to the "green canary."

But if not reversion, under what rubric shall we place the greenness of the goldfinch × canary hybrid? First it is to be recalled that the yellow canary is a green deprived of black pigment. When black pigment is added from any source it occupies the emptied spaces and so restores the "green" and the black. Consequently we find streaking on the sides of the body in the goldfinch-canary hybrid and black on tail and wings. But the canary contains also a mottling factor and so the hybrid is "green" in certain areas only. The other areas are yellow or else yellow to which the chocolate color has been added on the back, wing coverts, and sides, and to which red has been added on the face. The belly, which is white in the goldfinch, remains yellow in the hybrid.

How, then, shall we conceive the gametic formula of the goldfinch and the yellow canary? As the goldfinch contains black (*N*), red, and chocolate, its formula may be given as *N, R, C, m*, while that of the canary is *n, r, c, M*, contributing only the mottling character. Then the zygote gives *NRCM* as dominants, and the adult hybrid shows, on top of the yellow, black, red on the face and chocolate on the back and the sides.

The foregoing theory of the gametic constitution of the yellow helps, moreover, to explain the great variability of the hybrids—corresponding to the variability of the mottled offspring of yellow × green. As we have seen that in an extreme case the hybrid yellow × green is practically yellow, so likewise the hybrid yellow × goldfinch is occasionally, though rarely, entirely or almost entirely yellow except for the red on the face.

Finally, attention must be called to the principle of *localization* of unit-characters. Red is found almost invariably in the goldfinch hybrid, but always confined to the head region. Chocolate occurs in

the hybrid, if at all, only where it is present in the goldfinch. Black, on the other hand, is a color that belongs both to the wild canary and the goldfinch. The yellow canary has merely lost one factor necessary to the production of black in these situations where black occurs in the green canary. When black is introduced by the goldfinch it is laid down (1) in accordance with the goldfinch formula and (2) also in accordance with the green canary formula, but (3) both distributions are controlled by the variegation factor, so that black (like the other pigments) is laid down only over more or less circumscribed areas of the body.

Series IV.—HYBRIDS BETWEEN THE YELLOW CANARY AND OTHER SPECIES.

Canary fanciers have been very active in making "mules" between various species of finches. Besides the goldfinch, the linnet (*Fringilla linota*), the greenfinch (*Fringilla chloris*), and the siskin (*Fringilla spinus*) have been crossed with the canary.

The linnet is a prevailingly brown bird, with black, white-edged quill feathers and darker striping on wing coverts and sides of body. The hybrids with the yellow canary are said usually to be dark birds resembling the linnet. Mottled birds sometimes occur, linnet coloration showing in patches on the otherwise yellow background. (Blakston, 1880, 272). Here the brown of the linnet seems to dominate over the canary green, but the mottling factor of the yellow canary is active.

The greenfinch is olive-green above, yellowish-green below, has black remiges edged with yellow (forming a wing-bar) and black rectrices edged with olive-green, except the four outer tail feathers, which are edged with bright yellow. The hybrids are sometimes dark like the greenfinch, but "highly variegated" are common. Here, again, is seen the mottling factor of the canary.

The siskin is streaked greenish above anteriorly and yellowish posteriorly; below is light green in the male and white in the female. There is a yellow stripe over the eye. The sides of body and wing coverts are distinctly striped. The wings and tail are prevailingly black, but the base of the rectrices and a wing-bar and wing-bow are yellow. The hybrid with the yellow canary (plate 1, fig. 2) closely resembles the siskin—the dark beak, the yellow supraorbital stripe, the striping, even to the lower tail-coverts, are all present. In my hybrids the wing-coverts and rump are green as in the green canary. Here again the hybrid shows the so-called reversion phenomena. Mottling occurs in the hybrids under certain conditions, but the usual type is all dark (plate 3, fig. 6).

The foregoing descriptions show first that in all hybrids between the yellow canary and a finch there is a tendency to "reversion"—a

result that falls into the same category as the "reversion" of the goldfinch hybrid. In all cases the hybrids with the yellow canary are very variable and frequently show more or less of the canary yellow. This is due to the mottling factor of the canary to which reference has been so often made. That it is the yellow canary which contains the mottling factor and is the source of the variability of the hybrids is shown by the facts that (1) hybrids with the green canary do not vary in this fashion, and (2) hybrids between any two species of finches—of which many are bred by fanciers—are "cast in one mold."

D. SUMMARY AND CONCLUSION.

The history of the domestic canary shows that it has been intensely bred for only about 250 years and may therefore be regarded as a relatively recently acclimated species when compared with poultry that have been bred for over 2,000 years. Nevertheless distinctive characters have arisen which behave in Mendelian fashion.

Crest is dominant over plain head.

Baldness is a unit-character and is recessive to perfect crest.

The yellow canary is derived from the original "green" canary by the loss of black. It carries a mottling factor. Consequently when the yellow canary is crossed with a pigmented canary or with a finch the hybrids are mottled.

The mottling is not a fixed pattern. The spots vary in position and relative size—they may cover nearly the whole body or they may form a mere "ticking." The degree of mottling is inheritable. Ticking behaves as a unit-character.

Mottling is a heterozygous character and throws mottled, clear yellow and self-greens.

The principle of localization of the units of a complex plumage must be recognized. The cap of the Lizard canary, the red face of the goldfinch, the shoulder striping of the green canary are not only unit-characters but they occur only at their proper localities and in their proper forms in the body plumage. In mottled canaries the presence of black on the shoulder means striping, on the wing it means dead black, white-laced remiges, on the mid-breast it means a uniform olive color. The plumage of a yellow canary may be compared with a letter that has been written with invisible ink. Wherever the developer acts (*i. e.*, the black pigment of the green canary is added) that which is written appears with all of its idiosyncrasies.

Cold Spring Harbor, N. Y.,

September 28, 1907.

E. ALL MATINGS OF CANARIES, GIVING THEIR OFFSPRING.

(o) indicates that the bird was one of the original stock and is of unknown ancestry; (Y) yellow; (G) green; (N) black; (R) right; (L) left; (P) pied; (Pg) pied with a predominance of green; (Py) pied with a predominance of yellow; (g, y) after a number in "Mottled" Column, predominance of green or yellow color in plumage; (Cr) crested; (Ab) absence of crest; (Liz) lizard canary; (*) bald. The numbers assigned to parents and to offspring are those of their leg-bands. Figures in parenthesis tell how many offspring died young, before being banded. Superior figures refer to the notes in the last column, headed "Remarks."

PARENTS.											OFFSPRING.					
	MOTHER.					FATHER.					CREST.		PLUMAGE COLOR.			
Exp. No.	No.	Origin Exp. No.	Crest.	Color.	Used also in Exp. No.	No.	Origin.	Crest.	Color.	Used also in Exp. No.	Absent.	Present.	Yellow.	Green.	Mottled.	REMARKS.
401	7	o	ab	Y	505, 513, 614	8	o	ab	Y	512, 605	31		31			
402	10	o	ab	G		9	o	cr	G	504, 510, 608		44		44		
403	21	o	cr	Y		13	o	cr	Y	506, 508, 515	35	34	34, 35			
404	17	o	ab	G		16	o	ab	G		37, 38			37, 38		
405	19	o	ab	Y	604, 704	20	o	ab	Y			39, 40	39, 40			
501	4	o	ab	Y	509	37	404	ab	G	509, 616, 624	51, 52, 53 (+ 4 others)		51		52, 53	
502	44	402	cr	G		16	o	ab	G	404	55, 98	54, 56, 57, 87, 97		54, 55, 56, 57 87, 98		
503	3	o	cr	Y	511	40	505	ab	Y	511	(2)	58, 60 (+2)	58[1] (+1)		60[2]	[1]Exc. G nape [2]N spots on secondaries
504	6	o	cr	Y	510	9	o	cr	G	402, 510, 608	64	61, 62 (+4)			61, 62, 64	
505	7	o	ab	Y	401, 513, 614	34	403	cr	Y	513, 611, 710	65, 89	66, 67, 68, 90	65, 66, 67, 68, 89, 90			
506	12	o	cr	G		13	o	cr	Y	403, 508, 515		69*, 70*			69g, 70y	
507	18	o	ab	Y		46	o	ab	Gld Liz			71			71[1]	[1]Capped
508	11	o	cr	G	515, 603	13	o	cr	Y	403, 506, 515	74	72*, 73			72y, 73, 74	
509	4	o	ab	Y	501	37	404	ab	G	501, 616, 624	75, 76, 77, 78				75y, 76, 77, 78	
510	6	o	cr	Y	504	9	o	cr	G	402, 504, 608		79*, 80*, 81*, 82*			79, 80, 81, 82	
511	3	o	cr	Y	503	40	405	ab	Y	503	84, 85	83	83, 84[1], 85			[1]Slight ticking on L wing
512	101	o	ab	Sil Liz		8	o	ab	Y	401, 605	88, 99, 100				88, 99, 100y	
513	7	o	ab	Y	401, 505, 614	34	403	cr	Y	505, 611, 710	89	90	89[1], 90			[1]G patch on L nape
514	31	401	ab	Y		50	o	cr	G	613	92, 93	94, 95			92, 93, 94, 95	
515	11	o	cr	G	508, 603	13	o	cr	Y	403, 506, 508		96*			96	
601	12	o	cr	G	506	73	508	cr	P	708		(7)		(4)	(3)	
603	11	o	cr	G	508, 515	80	510	cr	P			176*, 177, 178		177, 178	176	
604	19	o	ab	Y	405, 704	62	504	cr	P		107, 108, 112, 191 192, 194, 205	111, 193*	107, 108, 110, 112		111, 112y, 191g 193y, 194, 205	
605	89	513	ab	P		8	o	ab	Y	401, 512	135, 136, 168, 169 170, 171 (+3)		168, 169, 170, 171 (+3)		135y, 136y	
606	39	405	ab	Y		68	505	cr	Y		113, 115, 116, 117 167, 172, 173, 174 175	114	113, 114, 115, 116[1] 117, 167, 172, 173[2] 174, 175[3]			[1]N spot on R wing [2]N spot on nape [3]N on breast
608	67	505	cr	Y		9	o	cr	G	402, 504, 510		163*, 164*, 165 166 (+1)			163, 164g, 165 166y (+1)	
609	84	511	ab	P		65	505	ab	Y		143, 144, 145, 146 211, 212, 213, 215		143[1], 144[2], 146 211, 212[3], 213[4] 215		145y	[1]N spot L eye [2]N " on nape [3]N " on top of head [4]N " " L side "

610	54	502	cr	G	. . . . .	61	504	cr	P	701	. . . . .	206, 207	. . . . .	207	206g	. . . . .
611	97	502	cr	G	. . . . .	34	403	cr	Y	505, 513, 710	138, 139 (+1)	. . . . .	(1)	. . . . .	138, 139	. . . . .
612	76	509	ab	P	. . . . .	51	501	ab	Y	. . . . .	201	. . . . .	. . . . .	. . . . .	201	. . . . .
613	55	502	ab	G	. . . . .	50	o	cr	G	514	119, 121, 179, 180 181, 182, 183	118	. . . . .	118, 119, 121 179, 180, 181 182, 183	. . . . .	. . . . .
614	7	o	ab	Y	401, 505, 513	39	405	ab	Y	. . . . .	122	. . . . .	122	. . . . .	. . . . .	. . . . .
615	53	501	ab	P	. . . . .	28	o	ab	G	. . . . .	123, 124, 195, 199 200, 217, 218, 219	. . . . .	. . . . .	199, 217, 218	123, 124, 195, 200 219	. . . . .
616	100	512	ab	P[1]	719	37	404	ab	G	501, 509, 624	(2)	. . . . .	. . . . .	. . . . .	(2)[2]	[1]Lizard, capped [2]Both capped
617	82	510	cr	P	. . . . .	79	510	cr	P	704	. . . . .	156* (+3)	. . . . .	156	. . . . .	. . . . .
618	52	501	ab	Py	. . . . .	75	509	ab	Py	. . . . .	103, 104, 150, 151 152, 208, 209, 210	. . . . .	104, 208	. . . . .	103, 150y, 151 152g, 210y, 209y	. . . . .
619	64	504	ab	Pg	. . . . .	85	511	ab	Y	. . . . .	130, 131, 132, 133 134, 137, 153, 154 155, 162, 220, 221	. . . . .	155, [162?], 221[1]	. . . . .	130, 131, 132y 133y, 134, 137y 153, 154, 220	[1]N on nape
620	69	506	cr	Pg	. . . . .	83	511	cr	Y	. . . . .	125, 214 (+1)	126* (+1)	(1)[1]	. . . . .	125, 126, 214y	[1]N spot
621	81	510	cr	P	. . . . .	58	503	cr	Py	. . . . .	188	127, 129, 189 190 (+1)	188[1] (+1)	. . . . .	127, 129, 189, 190y	[1]N patch at base of beak
622	74	508	ab	P	. . . . .	77	509	ab	P	. . . . .	105, 184, 185, 186 187 (+3)	. . . . .	105[1]	. . . . .	184, 185y, 186 187 (+3)	[1]Ticking on R remiges
623	78	509	ab	P	. . . . .	37	404	ab	G	501, 509, 616	140, 141, 142	. . . . .	. . . . .	140, 141	142	. . . . .
624	33	o	ab	G	. . . . .	87	502	cr	G	. . . . .	158, 160, 161	157	. . . . .	157, 158, 160, 161	. . . . .	. . . . .
701	207	610	cr	G	. . . . .	61	504	cr	P	610	297 (+2)	(1)	(1)	. . . . .	297 (+2y)	. . . . .
702	. .	o	cr	Y	. . . . .	269	o	cr	Py	. . . . .	326	327	326, 327 (+3)	. . . . .	. . . . .	. . . . .
703	67	10	cr	Y	608	166	608	cr	Py	. . . . .	255, 256, 302	253, 254, 303* (+3)	255, 256, 302, 303 (+2)	. . . . .	253y, 254y (+2)	. . . . .
704	19	o	ab	Y	405, 604	79	510	cr	P	617	. . . . .	257, 258*, 259* 304, 305	305[1]	. . . . .	257, 258, 259, 304	[1]N spot on head
705	127	621	cr	Py	. . . . .	125	620	ab	P	. . . . .	296, 337, 338	250*, 251*, 293 294, 295	251, 293, 294, 295 337	338	250, 296	. . . . .
706	126	620	cr	Py	. . . . .	214	620	ab	Py	. . . . .	. . . . .	274*, 275*, 276* 306	306	. . . . .	274, 275, 276	. . . . .
707	74	508	ab	P	622	206	610	cr	G	. . . . .	288	287	. . . . .	288[1]	287	[1]Primaries Y
708	138	611	ab	P	. . . . .	73	508	cr	P	601	308, 313	307, 309* (+2)	. . . . .	307, 313	308, 309y (+2)	. . . . .
709	111	604	cr	P	. . . . .	143	607	ab	Y	. . . . .	277, 278, 279, 280	. . . . .	277[1], 278, 279, 280	. . . . .	. . . . .	[1]N speck over L eye
710	97	502	cr	G	611	34	403	cr	Y	505, 513, 611	. . . . .	(3)	. . . . .	. . . . .	(3y)	. . . . .
711	164	608	cr	P	. . . . .	118	613	cr	G	. . . . .	. . . . .	298, 299	299	. . . . .	298	. . . . .
712	152	618	ab	G	. . . . .	215	609	ab	Y	. . . . .	310, 312	. . . . .	. . . . .	. . . . .	310, 312	. . . . .
713	178	603	cr	G	. . . . .	107	604	ab	Y	. . . . .	245, 331, 333, 334	243, 244, 332 335	335	. . . . .	243, 244, 245, 331g 333g, 334y (+1)	. . . . .
714	157	625	cr	G	. . . . .	240	o	cr	P	. . . . .	261	260, 262, 263 301 (+2)	(1)	261, 301	260, 262, 263 (+1)	. . . . .
715	184	622	ab	P	. . . . .	103	618	ab	P	. . . . .	. . . . .	. . . . .	. . . . .	. . . . .	(1y)	. . . . .
716	210	618	ab	Py	. . . . .	186	623	ab	Py	. . . . .	323, 324, 325	. . . . .	. . . . .	. . . . .	323 324, 325	. . . . .
718	132	619	ab	P	. . . . .	201	612	ab	P	. . . . .	246, 247	. . . . .	. . . . .	. . . . .	246g, 247g	. . . . .
719	100	512	ab	P	616	135	605	ab	P	. . . . .	282, 283	. . . . .	283	. . . . .	282y	. . . . .
720	193	604	cr	Py	. . . . .	169	605	ab	Y	. . . . .	. . . . .	252, 322	252, 322	. . . . .	. . . . .	. . . . .
721	339	o	ab	Y	. . . . .	209	618	ab	Py	. . . . .	270, 271, 272, 273 314, 315, 316, 317	. . . . .	270, 271, 272, 273 314, 317	. . . . .	315y, 316y	. . . . .
723	200	615	ab	P	. . . . .	142	624	ab	Py	. . . . .	289, 290, 291, 292 340	. . . . .	289, 290, 340	292	291	. . . . .
725	112	604	ab	Py	. . . . .	105	623	ab	Y	. . . . .	321	. . . . .	321	. . . . .	. . . . .	. . . . .
726	213	609	ab	Y	. . . . .	155	619	ab	Y	. . . . .	248, 249	. . . . .	248, 249	. . . . .	. . . . .	. . . . .
729	174	606	ab	Y	. . . . .	110	601	. .	Y	. . . . .	319	318, 320	318, 319, 320	. . . . .	. . . . .	. . . . .

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FIG. 1. CRESTED "GREEN" CANARY (NO. 118 ♂)
FIG. 2. CRESTED YELLOW CANARY, MEALY TYPE (NO. 67 ♀)

FIG. 3. HYBRID BETWEEN GOLDFINCH (FIG. 4) AND CRESTED YELLOW CANARY. TYPE OF FIG. 2 (NO. 203 ♂)
FIG. 4. EUROPEAN GOLDFINCH, FATHER OF NO. 203 (FIG. 3)

FIG. 5. MOTTLED OFFSPRING OF CANARIES OF TYPES OF FIGURES 1 AND 2. HIGHLY VARIEGATED TYPE (No. 61 ♂)
FIG. 6. HYBRID BETWEEN SISKIN AND CRESTED YELLOW CANARY (No. 264)

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